TRANSACTIONS
OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

Volume 21 Number 12 pp. 203–220 24 February 1988

Camaenid land snails (Gastropoda: Pulmonata) from the Eocene of southern California and their bearing on the history of the American Camaenidae

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Abstract. *Zachrysia fraterna,* new species, is described from the upper middle Eocene Friars Formation, San Diego County, California. All other records of *Zachrysia* are from Cuba, as Quaternary fossils or living. The presence of *Z. fraterna* implies forested land and a tropical climate with ample summer rainfall. Two Eocene species, described as *Helminthoglypta obtusa* from the Tejon Formation and *H.*? *stocki* from the Sespe Formation, are not Helminthoglyptidae but Camaenidae. Discoveries of extant Neotropical camaenid genera as Paleogene fossils in North America establish a middle Eocene minimum age for these genera and constrain hypotheses about the sources and timing of origin of the Caribbean biota. Recent and fossil distributions form a north-south generalized track from North America to the Caribbean region. As a family the Camaenidae show the "interrupted Tethyan" type of distribution. Links between the American and Australasian groups of Camaenidae are more likely to be found in Europe and western Asia than in the Pacific realm.

INTRODUCTION

The Camaenidae are a large family of pulmonate land snails with a discontinuous distribution. One branch of the family inhabits the West Indies, Central America as far north as Costa Rica, and Andean South America as far south as Peru. The other branch extends from eastern India and southern China through the Solomon Islands, south into the northern three-quarters of Australia, with a few taxa extending as far north as southern Japan (Solem 1979). Several recent studies have documented the presence of camaenid land snails in lower Tertiary strata of western and mid-continent North America (Solem 1978, 1979; Bishop 1979; Roth 1984).

In 1985 members of the Department of Paleontology of the San Diego Natural History Museum collected fossil invertebrates from a marine stringer in the predominantly nonmarine Friars Formation, of Eocene age, in southwestern San Diego County, California. Three taxa of nonmarine gastropods were present, including a well-preserved specimen that is conchologically indistinguishable from the modern camaenid genus *Zachrysia* Pilsbry, 1894. *Zachrysia* is otherwise known only from Cuba, as living species or Quarternary fossils. In addition, the type material of two southern Californian Eocene species originally assigned to *Helminthoglypta* Ancey, 1887, has been reviewed. With different degrees of certainty, those species are also assignable to Camaenidae.

The sources of the fossils discussed in this paper are shown in Figure 1. Figure 2 presents the correlation of rock units yielding camaenid fossils in western North America; age and geologic setting are discussed further below.

There is now enough material available to show that as early as middle to late Eocene time the American Camaenidae were differentiated into several genera of modern aspect and arrayed across at least the southern part of North America, perhaps roughly paralleling the remnants of the Tethyan seaway. The biogeographic history of the group since that time has consisted largely of a southward, and to some extent east-west, restriction to the present Caribbean region along with the development of a distinctive pattern of insular allopatry.

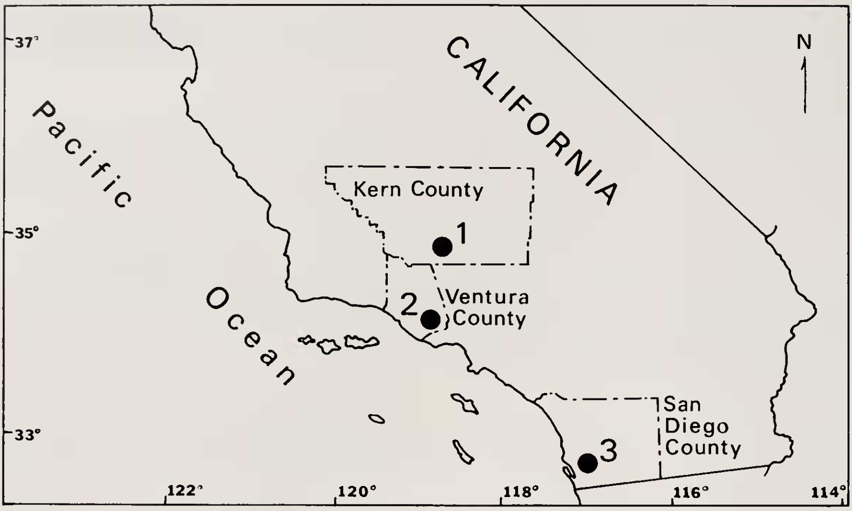


FIGURE 1. Map of southern California showing location of sources of material discussed herein. 1, Type Tejon Formation, Live Oak Creek; 2, Sespe Formation, Tapo Canyon; 3, Mission Valley and Friars formations, San Diego area.

Fortunately for paleontologists, the shells of American Camaenidae are usually diagnostic at the generic, and sometimes the subgeneric, level. The definitive anatomical work on the group (Wurtz 1955) did little to alter the earlier concepts of genera founded on conchological characters. With a few modifications after Solem (1966), Wurtz's anatomical study formed the basis for the phylogenetic analysis proposed by Bishop (1979) and accepted here without changes.

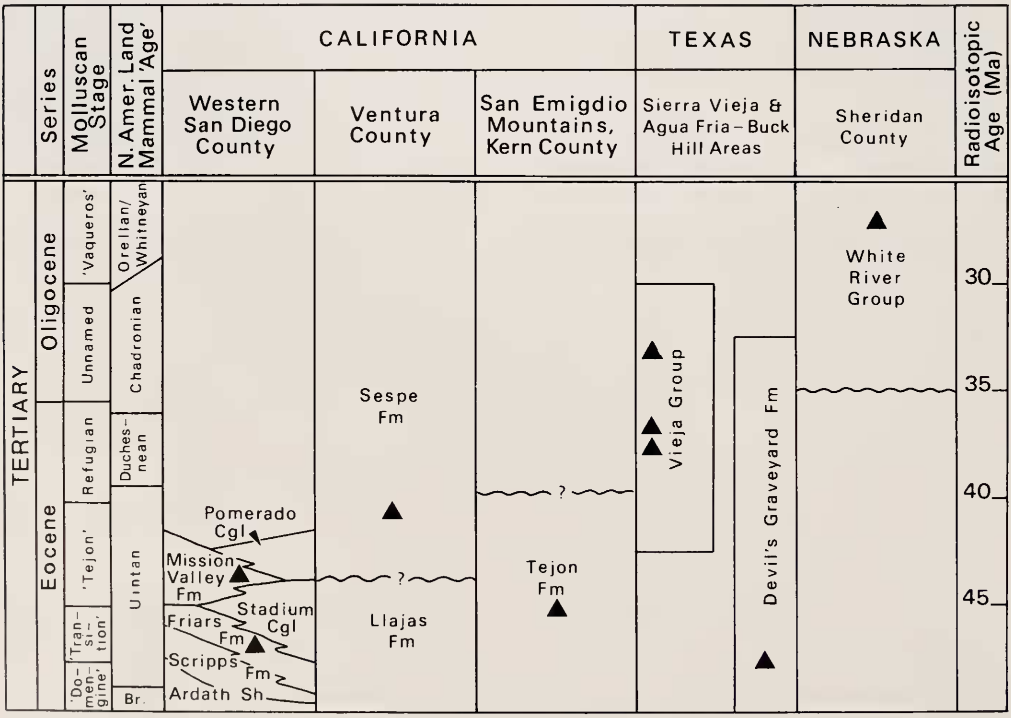


FIGURE 2. Correlation of Eocene and Oligocene formations in California, Texas, and Nebraska that have yielded camaenid land snails. Solid triangles indicate approximate stratigraphic positions of camaenid fossils.

The following abbreviations are used: CAS, Department of Geology, California Academy of Sciences; CIT, California Institute of Technology (collections now at Natural History Museum of Los Angeles County); LACMIP, Section of Invertebrate Paleontology, Natural History Museum of Los Angeles County; SDSNH, Department of Paleontology, San Diego Natural History Museum; UCMP, Museum of Paleontology, University of California, Berkeley.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797
Subclass Pulmonata Cuvier, 1817
Order Sigmurethra Pilsbry, 1900
Superfamily Camaenacea Pilsbry, 1895
Family Camaenidae Pilsbry, 1895
Zachrysia Pilsbry, 1894

Zachrysia Pilsbry 1894:97. Pilsbry 1929:581–606. Wurtz 1955:135–137. Zilch 1960:598.

Type species.—*Helix auricoma* Férussac, 1821, by subsequent designation (Pilsbry 1929:586). Recent, Cuba.

Generic diagnosis.—Shell white with brownish-yellow periostracum, depressed globose, with small spire and few, rapidly expanding whorls; the first 1.5 embryonic, polished, the first half whorl with extremely fine microscopic spiral lines, the next with fine axial riblets, the rest with oblique growth striae and extremely fine, dense granules, mostly arranged in irregular spiral lines. Last whorl rounded, somewhat flattened below, not umbilicate. Aperture very oblique, without teeth; peristome expanded; basal margin elongated, turned up and appressed (Zilch 1960, translation).

In some species all embryonic sculpture may be nearly obsolete (Pilsbry 1929). The genital system includes distinctive characters which are of course inaccessible on fossil specimens.

The several subgenera of *Zachrysia* are founded on characteristics of the genital system (Pilsbry 1929, Bonilla 1936, Wurtz 1955). Minutely decussate shell sculpture occurs only in the subgenus *Megachrysia* Pilsbry, 1929, but otherwise there are no conchological characters that discriminate the subgenera. The following fossil species is therefore assignable to the genus in the broad sense only.

The modern range of *Zachrysia* is limited to Cuba, with several human introductions elsewhere in the Caribbean region. The only other fossil record is "along the shore east of Punta San Juan de los Perros," Cuba (Pilsbry 1929:603), where specimens of *Z. auricoma* occur in a presumably Pleistocene or Holocene deposit.

Zachrysia fraterna, new species
Figures 3, 4

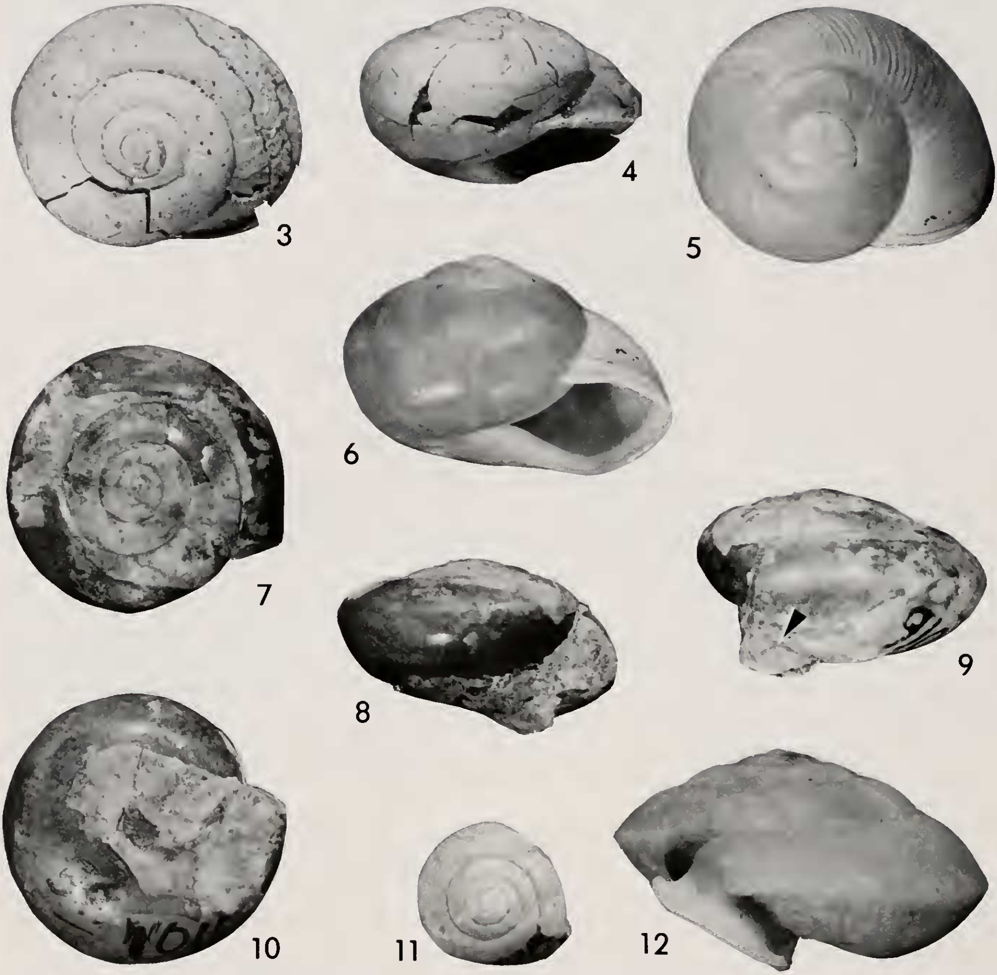
Holotype.—SDSNH 28388.

Type locality.—SDSNH Loc. 3278, San Diego County, California. Construction site at 4760 Murphy Canyon Road, San Diego (39°49′26″N; 117°07′05″W), exposing 15 m of Friars Formation and at least 8 m of overlying Stadium Conglomerate, elevation 71 m; collected by B. O. Riney, 23 February 1985. Friars Formation, upper middle Eocene. From blue-gray conglomeratic sandstones at the base of a 50–70 cm-thick graded bed, approximately 12 m below the Friars Formation-Stadium Conglomerate contact. A retaining wall now covers the collecting site.

Diagnosis.—A small, depressed-helicoid *Zachrysia* with 4.8 whorls, attenuated base, smooth, sinuous radial riblets, and reflected but not greatly thickened lip.

Etymology.—The species is named for the Friars Formation (*fraterna*, L., brotherly).

Description.—Shell small for the genus, thin, inflated, depressed-helicoid, imperforate, broadest above middle of body whorl; base attenuated. Spire low, weakly convex in profile; suture moderately impressed. Embryonic whorls 1.4, smooth. Early teleo-



FIGURES 3–12. 3, 4, *Zachrysia fraterna*, n. sp., holotype, SDSNH 28388, top and apertural views; major diameter 23.5 mm. 5, 6, *Zachrysia auricoma havanensis* (Pilsbry), Holocene, Havana, Cuba, top and apertural views; major diameter 25.7 mm (author's collection). 7–10, *Labyrinthus obtusus* (Anderson and Hanna), holotype, CAS Geology Type Collection 1016, top, apertural, lateral, and basal views; diameter 16.0 mm; arrowhead points to basal constriction. 11, *Labyrinthus*(?) sp., SDSNH 32044, top view; diameter 12.6 mm. 12, *Labyrinthus manueli* Higgins, Holocene, Mera, Ecuador, lateral view; diameter 21.7 mm (CAS).

conch whorls irregularly corrugated by low growth rugae which grade, from about beginning of fourth whorl on, into acute, raised, more or less regularly spaced, sinuous radial riblets. Riblets convex in direction of growth on shoulder of whorl, retractive at periphery, shallowly concave below periphery, and almost straight where they cross the base; riblets on body whorl subequal in strength and spacing, triangular in cross-section, smooth, or obscurely beaded by faint wrinkling below suture. Periphery of penultimate whorl rounded-subangular, grading to broadly rounded on body whorl. Last ⅛ whorl descending steeply to aperture, apico-basally compressed, constricted behind lip. Aperture broadly ovate, markedly oblique, at angle of 60° to vertical; lip expanded and strongly reflected, curving backward over pre-apertural constriction. Parietal wall calloused, striate, reflecting underlying riblets. Basal lip rather wide, compressed upward, thickened, columellar portion (all preserved) with a shallow sulcus running outward from umbilical region. Major diameter (incomplete) 23.5 mm, minor diameter 19.3 mm, height 16.9 mm; whorls 4.8.

Discussion.—*Zachrysia fraterna* differs from all other species of the genus in having 4.8 whorls. As described by Pilsbry (1929), modern Cuban species have from 4 to 4.5

whorls. However, the low-helicoid shape, rapidly expanding whorls, and attenuated base rapidly sloping from the periphery to the columellar area leave no doubt that this is a species of *Zachrysia.* The sinuous radial sculpture is also typical of the genus. The lower edge of the aperture of the holotype is broken, but the remaining columellar portion shows that the basal lip was thickened and compressed upward as in modern species and may have had a shallow sulcus running along its length. There is no indication whether or not denticles were developed on the basal lip.

The holotype has been slightly compressed in a direction normal to the plane of the aperture, accentuating the difference between major and minor diameters.

The shell structure consists of (1) an outer, radial crossed-lamellar layer with first-order lamellae parallel to the direction of growth; (2) a middle, concentric crossed-lamellar layer with first-order lamellae at right angles to the first; and (3) an inner, concentric crossed-lamellar layer (terminology after MacClintock 1967). The contact between the outer and middle layers is gradational, with the first-order lamellae undergoing a 90° rotation in the plane of the shell surface. The contact between the middle and inner layers is sharp and unconformable, with a tendency for the two layers to separate at the site of a break. The outer layer makes up about 20% of the total thickness of the shell. The middle and inner layers each make up about 40%, but the thickness of the inner layer is variable. Thickening around the peristome results mainly from augmentation by the inner layer. Modern *Zachrysia auricoma* shows the same sequence and relative thickness of shell layers, supporting the generic assignment.

No single modern taxon stands out as conchologically most similar to *Z. fraterna,* but *Zachrysia auricoma,* particularly the small-shelled subspecies *Z. a. havanensis* (Pilsbry, 1894), is generally similar in size and outline (Figures 5, 6). The periphery of the penultimate whorl of *Z. fraterna* is less broadly rounded and is almost angulate where the last whorl begins its descent to the aperture. The angulation is not as acute as in *Zachrysia torrei* (Henderson, 1916) (Pilsbry 1929:pl. 29, figs. 8, 10).

Based on the scanty data of this one Eocene specimen and the twenty or so extant species, one can infer that the trend of shell evolution in *Zachrysia* has been toward (1) larger overall size, (2) reduced number of whorls, and (3) more rapidly expanding whorls, producing a larger shell at a given whorl number. At the same time, the overall shape has held remarkably constant.

Associated fauna.—The holotype (and only specimen) was found in a marine sandstone stringer in the mainly nonmarine Friars Formation, associated with a moderately diverse nearshore molluscan assemblage dominated by *Pachydesma* sp., cf. *P. kelloggensis* (Clark and Woodford, 1927), *Tellina soledadensis* Hanna, 1927, and *Turritella uvasana* Conrad, 1855, *sensu lato.* Rare estuarine molluscan taxa, including *Loxotrema turritum* Gabb, 1868, and *Nerita triangulata* Gabb, 1869, were also present (T. A. Deméré, *personal communication* 1986). Two other taxa of nonmarine mollusks were present: (1) an almost planispiral gastropod 6.3 mm in diameter and 2.3 mm high, consisting of 3.4 whorls, somewhat suggesting the ammonitellid genus *Megomphix* Baker, 1930, but not further identifiable because the surface sculpture is not preserved; and (2) two partial spires of lenticular pulmonate land snails, 12.9 and 13.6 mm in maximum preserved diameter, of 4.7 and 4.2 whorls respectively, with very oblique growth striae and subangular periphery. These are discussed under *Labyrinthus*(?) species, below.

Labyrinthus Beck, 1837

Labyrinthus Beck 1837:33. Wurtz 1955:114–117 (in part). Zilch 1960:602–603 (in part). Solem 1966:37–44.

Ambages Gude 1912:21–23. Wurtz 1955:114.

Type species.—*Helix labyrinthus* "Chemnitz" Deshayes, 1838 (=*Helix otis* Lightfoot, 1786), by subsequent designation (Herrmannsen 1846:569). Recent, Costa Rica to Colombia.

Generic diagnosis.—Shell small to large; depressed globose to planulate; surface sculpture of growth wrinkles or granulations, but never ribbed; spire nearly flat to moderately elevated; periphery rarely rounded, usually acutely angulated or protrudingly keeled; umbilicus partly (rarely completely) closed by extension of basal and parietal lips; aperture strongly deflected near end of body whorl, partially obstructed in adult by gross expansion of lips and development of various denticles and lamellae; parietal lip raised and with reflected edge, basal and palatal lips thickened and strongly reflected; parietal wall with single short to long, curved to sinuated lamella that stops short of or merges with the elevated parietal lip; basal lip straight to sinuated, normally with one lamellar knob marking its outer boundary, occasionally with a second inner knob; lower palatal lip with single crescentic lamella, hooked lamellar tooth, large transverse lamellar plate or y-shaped bifid tooth with deep indentation behind lip; upper palatal lip with weak lamella or triangular knob in a few species (Solem 1966).

Solem's (1966) monograph gave generic rank to *Isomeria* Albers, 1850, which both Wurtz (1955) and Zilch (1960) had treated as a subgenus of *Labyrinthus.* While noting that anatomical evidence did not support separation of *Labyrinthus* and *Isomeria,* Solem gave them coordinate rank because of shell characters and altitude ranges.

Although it is not stated explicitly, Bishop's (1979) figures 20–21 show that he used "*Labyrinthus*" in the inclusive sense of Wurtz (1955) and Zilch (1960).

In spite of these differing opinions as to taxonomic rank, all authors agree that *Labyrinthus* plus *Isomeria* form a monophyletic group distinct from the rest of the American Camaenidae. It is to be expected that fossil species may be found that cannot be assigned to one or the other but only to a *Labyrinthus-Isomeria* lineage. Note that two Holocene species, *Isomeria minuta* Solem, 1966, and *I. inexpectata* Solem, 1966, are regarded as intermediate in shell characters (Solem 1966:127–128).

The modern range of *Labyrinthus* extends from northern Costa Rica south to Madre de Dios, Peru, east to Caracas, Venezuela, and Pará, Brazil (Solem 1966). No other fossil occurrences are known, although "Camaenid, genus and species indet." of Roth (1984:210–211, figs. 29–31) shows some similarity to *Labyrinthus* and *Isomeria.*

Labyrinthus obtusus (Anderson and Hanna, 1925)
Figures 7–10

Helminthoglypta obtusa Anderson and Hanna 1925:142–143, pl. 3, figs. 12, 13. Henderson 1935: 141. Pilsbry 1939:66.

Holotype.—CAS Geology Type Collection 1016.

Type locality.—Kern County, California. Live Oak Creek. Collected by M. A. Hanna, 1922. Tejon Formation, Eocene.

Description.—The holotype is an internal mold with original shell material adhering; the shape is roughly lenticular, flatter above and more deeply convex below the periphery. The external surface appears to be well preserved. The protoconch and spire are smooth and unsculptured. The body whorl is sculptured with traces of oblique growth striae. There are 4.75 whorls preserved, but there were probably about five originally. The whorls are closely coiled, not rapidly expanding; the slight elliptical eccentricity visible in top view is probably the result of post-mortem compression. The whorl cross-section is lunate; the parietal wall is missing. The base is narrowly umbilicate, the umbilical region filled with matrix that shows the impression of an expanded, reflected columellar lip (now missing) that must have covered or nearly covered the umbilicus. The suture is well marked and there is no trace of reabsorption of internal whorl partitions; i.e., *L. obtusus* is a pulmonate, not a prosobranch. Only the basal part of the peristome is preserved but that is thickened and reflected. Just in back of the peristome the base of the body whorl is strongly constricted upward.

Diameter of holotype (incomplete) 16.0 mm, height 9.6 mm.

Discussion.—The distinct upward constriction of the base of the body whorl immediately behind the aperture, the thickened and reflected peristome, and the lenticular profile, more deeply convex below the angulate periphery, all indicate assignment to

Labyrinthus. A specimen of *Labyrinthus manueli* Higgins, 1872, is illustrated for comparison (Figure 12); the similarities are most apparent in lateral view.

Anderson and Hanna (1925) construed *Helminthoglypta* rather broadly and included species that would now be allocated to *Monadenia* Pilsbry, 1890. The shells of most *Monadenia* species are pustulose or finely spirally striate; they have distinctive protoconch sculpture of granules or clothlike texturing (Roth 1981). None has a basal constriction behind the aperture.

Helminthoglypta includes species with shells of moderate to large size, helicoid or depressed, with conic or low spire, open or covered umbilicus, and periphery rounded to angular in the subadult (Pilsbry 1939). A wide range of shell forms is found, from globose-conic and higher than broad to nearly planispiral. In all, however, the peristome is reflected simply, without being preceded by a basal constriction.

Several Holocene species of *Labyrinthus* become adult in the 15–20 mm diameter size range, although most are larger (to 60 mm). In all modern species the basal constriction is pronounced and the aperture furnished with various denticles and lamellae. Because the aperture of the holotype of *L. obtusus* is incomplete and the parietal wall is missing, no more detailed comparison with the modern species groups of *Labyrinthus* is possible.

Labyrinthus(?) species
Figure 11

Referred material and locality.—Two specimens, SDSNH 32044; from SDSNH Loc. 3278, San Diego County, California. Construction site at 4760 Murphy Canyon Road, San Diego (39°49′26″N; 117°07′05″W), exposing 15 m of Friars Formation and at least 8 m of overlying Stadium Conglomerate; elevation 71 m; collected by B. O. Riney, 23 February 1985. Friars Formation, upper middle Eocene. From blue-gray conglomeratic sandstones at the base of a 50–70 cm-thick graded bed, approximately 12 m below the Friars Formation-Stadium Conglomerate contact.

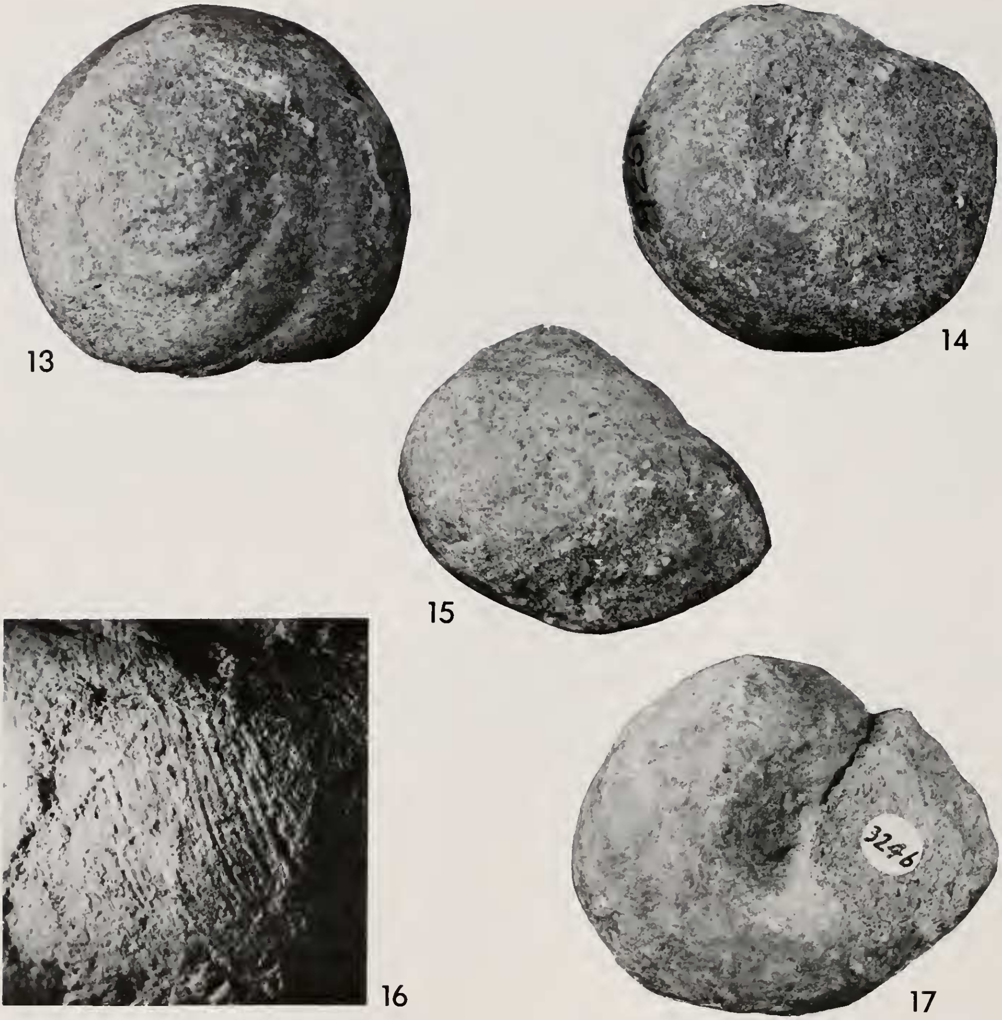
Description.—The material consists of two partial spires (with some internal whorls present) of lenticular land snails, 12.9 and 13.6 mm in maximum preserved diameter, consisting of 4.7 and 4.2 whorls respectively. The specimens are immature, without thickened lip, constricted body whorl, or other characters of terminal growth. The shell is more deeply convex below the subangular periphery. The whorls are closely coiled, not rapidly expanding; the whorl cross-section was apparently lunate. The base and umbilical region are not preserved. The suture is well marked and there is no indication of reabsorption of internal whorl partitions; i.e., they are pulmonates, not prosobranchs. The protoconch apparently consists of 1.5–1.7 whorls but is not well differentiated from the neanic whorls. The only sculpture consists of low, oblique growth rugae. Both specimens are slightly elliptical in top view, probably due to post-mortem distortion.

Discussion.—Without specimens showing the thickened and reflected lip of maturity, it is not possible to allocate this material more securely. However, the characters preserved—tight coiling, the general absence of sculpture other than growth rugae, the low spire, and greater convexity below the subangular periphery—are consistent with *Labyrinthus* and similar to *L. obtusus* from Kern County. The two specimens are smaller at a given whorl than the holotype of *L. obtusus*; the protoconchs are slightly smaller, and the growth rugae stronger.

Genus uncertain
[Camaenidae] *stocki* (Hanna 1934)
Figures 13–17

Helminthoglypta? *stocki* Hanna 1934:539, text-figs. 1–3a. Pilsbry 1939:66.

Type material and locality.—Holotype: LACMIP 4261 (formerly CIT 3244), from CIT vertebrate paleontology locality 180, Ventura County, California. Tapo Canyon, north of Simi Valley. Sespe Formation, lower upper Eocene. Two paratypes, LACMIP



FIGURES 13–17. [Camaenidae] *stocki* (Hanna). 13–15, holotype, LACMIP 4261, top, basal, and apertural views; diameter 38.0 mm. 16, 17, paratype, LACMIP 4262, detail of sculpture on body whorl and basal view; diameter 44.0 mm.

4262 and 4263 (formerly CIT 3246 and 3245, respectively), from same locality as holotype.

Referred material and locality.—UCMP loc. D-7811, San Diego County, California. At intersection of Lake Murray Blvd. and Dallas Street behind the Jack-in-the-Box drive-in (W½ SE¼ sec. 7, T. 16 S, R. 1 W, San Bernardino Base and Meridian); elev. 190 m [625 ft]. Mission Valley Formation, upper middle Eocene. This is the same as UCMP vertebrate locality V-6893, the Jack-in-the-Box locality of Golz and Lillegraven (1977) and other vertebrate workers.

Description.—The holotype and two paratypes are internal molds with thin partial crusts of recrystallized shell material, and a matrix of reddish and greenish lithic wacke. Patches of external sculpture are preserved on the last whorl of the holotype and paratype LACMIP 4262; they consist of fine, raised, axial riblets oblique to the direction of spiral growth, apparently parallel to lines of growth (Figure 16). The riblets do not anastomose, and each evidently retains its distinctness across the whorl. The apices of the shells are not well preserved. Hanna (1934) estimated about 6.5–7 whorls, but I judge only about five to be present. The whorls are closely coiled and do not expand rapidly. The whorl cross-section was apparently higher than broad, and ovate to sub-

TABLE 1. Measurements of type specimens of [Camaenidae] *stocki* (Hanna 1934).

	Holotype LACMIP 4261	Paratype LACMIP 4262	Paratype LACMIP 4263
Diameter:	38.0 mm	44.0 mm	36.7 mm
Height:	36.2	29.9 (skewed)	26.0

lunate. The base is umbilicate, best shown by paratype LACMIP 4262 (Figure 17). There is no obvious change in direction of growth of the last whorl, so it is uncertain whether or not these are mature shells. No obvious apertural modifications are present, although in paratype LACMIP 4262 the umbilicus appears to grade into a transverse basal groove like that characteristic of many New World Camaenidae (Solem 1978).

The suture is well marked, and below the suture the whorls show a narrow, steplike shoulder with a rounded outer edge. The shoulder is particularly evident on the internal molds, reflecting a general thickening of the shell toward the suture, but it is not solely an internal feature, also being present where shell material and external sculpture are preserved. Shell dimensions are summarized in Table 1.

The two referred specimens are internal molds with impressions of external sculpture in a matrix of light grayish tan lithic wacke. Their maximum diameter, with some deformation, is 30–35 mm. One has slightly more than five whorls; the other lacks the upper spire and the whorls cannot be counted. The better-preserved specimen shows clearly the sculpture of radial riblets, the narrowly shouldered whorls, and the umbilicate base of [C.] *stocki*. The body whorl is weakly dilated just behind the aperture and the peristome appears to have been moderately turned outward.

Discussion.—The evidence for taxonomic assignment of [Camaenidae] *stocki* is less satisfactory than that in the preceding cases. Finding of adult specimens with more shell material and the adult aperture preserved would greatly improve matters.

Hanna (1934) originally assigned the species to *Helminthoglypta* with doubt, although remarking that the essential characters of that genus were apparent. The only living species compared was the large form described about the same time as *Helminthoglypta tudiculata rex* Church and Smith, 1938. In 1933, Hanna had been one of the collectors of the type lot of that Holocene subspecies. Now known as *H. allyniana rex,* it has a much more depressed shell, with whorls expanding more rapidly, and the malleated sculpture typical of the *H. tudiculata* group of taxa. The umbilicus is narrow and almost covered by the expanded inner lip. The suture is moderately impressed; there is no trace of the narrow shoulder evident in [C.] *stocki.*

As noted above, *Helminthoglypta* includes a wide range of shell shapes. In no species, however, is there a narrow, steplike shouldering of the whorl below the suture.

The sculpture in *Helminthoglypta* consists of simple growth lines, malleation, papillae, or close, regular axial ribbing that is broken into granules by oblique, diverging grooves. Often more than one of these types of sculpture are present on the same shell. Raised axial riblets like those of [C.] *stocki* are not known in *Helminthoglypta.*

No other extant genera of Helminthoglyptidae match any better. Among large, globose or trochoid forms, *Humboldtiana* Ihering, 1892, has rapidly expanding whorls sculptured with coarse, granulose wrinkles. *Lysinoe* Adams and Adams, 1855, has sculpture of fine, discrete papillae on an otherwise smooth shell, or a malleated surface; its whorls are unshouldered and expand at a greater rate. *Monadenia* includes smooth shells and ones with strong, persistent papillation. The larger species of *Leptarionta* Fischer and Crosse, 1870, have a glossy or silky surface with growth lines scarcely evident in relief. *Polymita* Beck, 1837, likewise consists of smooth-shelled species.

The only modern genus of Helminthoglyptidae that shows comparable sculpture in some species is *Hemitrochus* Swainson, 1840, of southern Florida and the Antilles. Species of *Hemitrochus* have medium-sized to small, compact shells, often with a narrow, obliquely entering umbilicus. The shell of [C.] *stocki* is much larger than any of these, and the umbilicus seems to have been broadly open.

The American camaenid genus *Polydontes* Montfort, 1810, and the Australian camaenid genera *Xanthomelon* Martens in Albers, 1860, *Thersites* Pfeiffer, 1856, and *Hadra* Albers, 1860, include species that combine in one way or another the features of globose shell, slowly expanding whorls, narrow, steplike shoulder with emphasized suture, and fine but prominent radial ribbing. Although differing in its shagreened microsculpture and the absence of an umbilicus, the Neotropical camaenid *Polydontes* (*Luquillia*) *luquillensis* (Shuttleworth, 1854) is suggestively similar. For the present, however, [C.] *stocki* is assigned to family only, not to any specific genus. [Those who insist on a generic epithet are, of course, perfectly free to cite this taxon as *Polydontes*(?) *stocki*. I may be wrong in trying to bend nomenclatural practice in this way to express shades of uncertainty. Note that if the taxon had not already been formally named, we could simply cite it as "Camaenid, genus and species indet." The binomial system forces us to combine the two essentially distinct activities of identification and classification. "*Helminthoglypta*" *stocki* (with quotes) is an unsatisfactory form of citation because the species is not helminthoglyptid. And the old expedient of naming a new genus is not justified by the information available from the specimens.]

Age and Correlation

There are no radiometric dates associated with late Eocene terrestrial faunas in southern California. Age assignments of the formations that yielded the camaenid land snails discussed here are based on stratigraphic relationships to marine beds and faunal correlations with fossil mammals from the western interior (Figure 2).

Correlations of the Ventura and San Diego County Eocene formations are based on Golz and Lillegraven (1977), Lillegraven (1979), Givens and Kennedy (1979) and information supplied by T. A. Deméré (*personal communication* 1986). Fossil mammals in the Tapo Canyon Local Fauna indicate correlation with the Myton Member ("Uinta C" level) of the Uinta Formation of northeastern Utah and with the "Tejon" molluscan stage of the Pacific Coast marine megafossil chronology. The vertebrate fauna of the Mission Valley Formation is probably correlative with assemblages from the type section of the Tepee Trail (=Wagon Bed) Formation in Fremont County, Wyoming, the "Uinta B" level of the Uinta Formation, and the "Tejon" Stage. Most vertebrate remains from the Friars Formation have been found high in the formation and have been correlated with the "Uinta B" level and the "Transition" molluscan stage.

Fossil marine mollusks found in association with *Zachrysia fraterna* at SDSNH loc. 3278 include *Ficopsis remondii crescentensis* Weaver and Palmer, 1922, *Molopophorus antiquatus* (Gabb, 1864), *Neverita globosa* Gabb, 1869, *Eocernina hannibali* (Dickerson, 1914), "*Spisula*" *bisculpturata* Anderson and Hanna, 1925, and *Tellina soledadensis*. These taxa have stratigraphic ranges that typically overlap only within the "Transition" molluscan stage (Givens and Kennedy 1979), indicating that the type locality of *Z. fraterna* is of middle Eocene age (Lutetian; approximately 45–46 Ma before present). Flynn (1986) has recently shown that reversed magnetism in the main body of the Friars Formation represents magnetic polarity Chron C20R (approximately 46–48 Ma before present).

The age of the type locality of *Labyrinthus obtusus* is less certain. The Tejon Formation consists of marine sediments deposited during a major eastward transgression during the early, middle, and possibly late Eocene, followed by a westward regression in the late Eocene (Nilsen and Link 1975). The holotype was said to be "embedded in the typical hard Type Tejon sandstone with marine forms" in the canyon of Live Oak Creek (Anderson and Hanna 1925) but the exact part of the section where it was found is not known. Marks (1943) assigned the entire section of the Tejon Formation exposed in Live Oak Canyon to the Liveoak Shale Member, which has yielded Ulatisian and Narizian (middle to upper Eocene) foraminifers (Nilsen and Link 1975). A more recent interpretation of the stratigraphy (Nilsen and Link 1975: fig. 6) indicates that the subjacent Uvas Conglomerate Member (containing "Transition" Stage megafossils) and the superjacent Metralla Sandstone Member (containing "Tejon" Stage megafossils) may be present in Live Oak Canyon as well. In light of its nearshore deposition and abundant megafossils, the Uvas Conglomerate Member may be the most likely source of the holotype of *L. obtusus* (L. R. Saul, *personal communication* 1987).

Paleoecology and Paleoclimate

The average rate of evolutionary change expressed in the shell morphology of land mollusks is slow. Many modern genera appear first in upper Cretaceous or Paleogene strata with species that are virtually indistinguishable from their living congeners. If morphologic change is accepted as a fair sample of total evolutionary change, then land snail fossils can be viewed with confidence as indicators of ancient environments (Roth 1984).

The present-day climates of Kern, Ventura, and San Diego counties, California, are temperate, equable, and summer-dry. At Bakersfield, 50 km north of the type locality of *Labyrinthus obtusus,* the mean annual temperature is 18.4°C and there is a 20.4°C annual range of temperature; mean annual precipitation is 16.2 cm, less than 2.0 cm falling between May and October (Elford 1970). At San Diego the mean annual temperature is 17.3°C and the mean annual range is 9.3°C; mean annual precipitation is 26.4 cm, less than 2.4 cm falling between May and October. At Ventura, the mean annual range of temperature is only a few degrees greater; annual precipitation is 36.1 cm, 1.6 cm falling between May and October.

In the middle to late Eocene a system of coastal lowlands connected these areas and may have communicated with the western interior as well (Lillegraven 1979: fig. 2b). The San Joaquin Basin was flooded by a major marine transgression, the Transverse Ranges did not yet exist as an east–west feature, and the Peninsular Ranges had yet to migrate some 365 km northwest along the west side of the San Andreas fault system (Link *et al.* 1979, Lillegraven 1979, Nilsen and McKee 1979). The land mollusks indicate that the entire region from present-day Kern to San Diego counties was within a single zone of seasonally dry tropical forest.

Frakes and Kemp's (1972) reconstruction of Eocene global weather patterns (40–48 Ma before present) indicates that the southern margin of North America, bordering the Caribbean limb of the Tethyan seaway, had a monsoonal climate. The west coast of North America had a wet climate and warm marine temperatures. The area was free from the upwelling that modulates summer temperatures along the west coast today (Scotese and Summerhayes 1986).

Eocene strata in the San Diego area represent a complex of depositional environments including coastal plain, lagoonal, fan-delta, and paralic facies, near the mouth of a major river system (Kennedy and Moore 1971, Howell 1975, Link *et al.* 1979). Marine and nonmarine conditions alternated; a coastline was never far away.

The La Jolla and Poway Groups (which include the Friars and Mission Valley Formations) rest unconformably on Cretaceous and older rocks that are weathered to a lateritic paleosol. This paleosol probably developed in a humid, tropical climate with over 130 cm annual precipitation, an average annual temperature around 20–25°C, and lush rainforest vegetation (Peterson *et al.* 1975). (These authors refer to it as a "pre-Eocene" paleosol, but it could equally well be just slightly older than the overlying sediments and as young, in part, as middle Eocene.) Both the Friars and Mission Valley Formations, however, contain calcareous layers interpreted as caliche deposits. These would most likely have formed under semi-arid conditions with annual precipitation under 65 cm and seasonally distributed (Peterson *et al.* 1975, Peterson and Abbott 1979). Caliches are more common in the Mission Valley Formation than in the Friars Formation (Lillegraven 1979). Apparently middle to late Eocene was a time of transition locally from abundant rainfall (as in the modern equatorial belt of lateritic soils) to diminished rainfall and seasonal drought. Under the latter conditions the vegetation probably resembled modern steppe or savanna, with drought-resistant trees and shrubs.

Clast-composition of the Ballena Gravels to the east, deposits of the Eocene rivers that drained into the San Diego delta (Steer and Abbott 1984), suggests infrequent high-energy transport. This is interpreted as the result of major, seasonal flash floods in response to tropical storms dropping great amounts of rain on the mountains to the east (Lillegraven 1979, Steer and Abbott 1984). For much of the year, however, the rivers probably experienced only minor flow.

Today the native range of *Zachrysia* is limited to Cuba. Snails of this genus are inhabitants of humid and generally rocky forest, where they are found on rocks and cliffs, tree trunks, or on the ground (Pilsbry 1929). In typical humid weather they are often active by day, crawling on the ground, climbing trees to a height of 2–3 m, or wandering over rocks and cliffs. In dry periods they temporarily estivate. Pilsbry's (1929) observation that, with the exception of *Z. auricoma, Zachrysia* do not survive for long when confined in a dry box suggests that they have limited ability to resist desiccation.

Zachrysia provisoria (Pfeiffer, 1858) and *Z. auricoma* have been introduced into Florida (Pilsbry 1939, Dundee 1974); *Z. provisoria,* at least, has become established in Dade, Monroe, and Broward counties (J. E. Deisler, *personal communication* 1986). *Zachrysia provisoria* is established as an introduction in the Bahamas (Clench 1952, Deisler and Abbott 1984), and *Z. auricoma havanensis* in Puerto Rico (van der Schalie 1948). Wurtz (1955) mentioned that the genus had been introduced to the Canal Zone, without giving further particulars. The success of these introductions indicates that the restriction of *Zachrysia* to Cuba is not merely due to the absence of suitable conditions elsewhere.

The modern range of *Zachrysia* is consistent with (1) tropical climate, equable and frost-free but with some winter cooling (Seifriz 1943); (2) precipitation between 80 and 200 cm annually, ample in summer but with a pronounced winter dry season (Seifriz 1943, Portig 1976); and (3) forested land, but not necessarily rainforest. The greatest diversity of species is recorded in mountainous regions, which are also the wettest areas. It is not clear from published collection records whether this is mainly sympatric or allopatric diversity. The observations of Pilsbry (1929) and van der Schalie (1948) indicate that at least *Z. auricoma* may tolerate open, drier conditions fairly well.

At present *Labyrinthus* has an extensive range from Costa Rica to Peru and the Amazon basin of Brazil. Perhaps a third of the species have altitude ranges of more than 900 m (Solem 1966). This broad distribution and the scarcity of ecological information limit the usefulness of the genus for paleoclimatic interpretation. Material collected by Solem (1966) in Panama was taken in "reasonably heavy forest." Baker (1926) found Venezuelan species in dense forest under logs and debris or in humus near rocky ledges. The geographic range of *Labyrinthus* is broad enough to take in many tropical forest types; at least some of the regions experience a winter dry season.

The fragile shells of *Zachrysia, Labryinthus*(?), and the unidentified planispiral species from the Friars Formation probably underwent only minimal transport before being deposited in a protected, shallow marine setting. They may have been living in a humid forest fringing a coastal lagoon. It is less likely that they were caught up in flash flooding and transported from the interior. Heavily vegetated coastal belts persisted into the later Eocene (Lillegraven 1979). In these belts the effects of seasonal drought may have been minimized, permitting a diverse land snail fauna to thrive.

The laterally intertonguing and partly subjacent Scripps Formation, representing submarine canyon fill or inner fan deposits (Link *et al.* 1979), has yielded the prosobranch land snail "*Helicina*" *dallasi* (Hanna, 1926), likewise indicative of tropical conditions (Roth and Pearce, in press).

The Sespe Formation of Ventura County is of fluvial origin and thought to have been deposited for the most part near sea level (Lillegraven 1979). Paleoclimatic studies are lacking, although time-equivalent marine faunas in the area indicate tropical to subtropical marine conditions. If better material of [Camaenidae] *stocki* confirms its similarity to *Polydontes luquillensis,* then paleoclimatic inferences could be based on the study by Heatwole and Heatwole (1978) of *P. luquillensis* in Puerto Rico.

The general climatic inferences drawn from *Labyrinthus* above would also apply

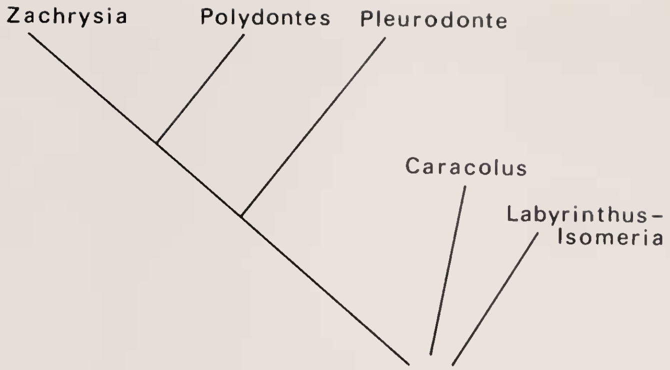


FIGURE 18. Phylogenetic hypothesis (cladogram) for the genera of American Camaenidae, after Bishop (1979), q.v. for pattern of apomorphies.

to the Kern County setting of *L. obtusus.* The holotype of *L. obtusus* was found with a marine invertebrate fauna containing species of *Ficus, Latirus, Niso,* and *Pteria*—genera that today are either exclusively or predominantly tropical in distribution.

HISTORY OF THE AMERICAN CAMAENIDAE

The origin of the Caribbean terrestrial biota has been the subject of considerable debate in recent years (Hedges 1983). The principal dichotomy has been between the view, on the one hand, that the major events of colonization and radiation occurred in post-Oligocene time, predominantly involved over-water dispersal, and can be visualized on an essentially modern map of the distribution of land masses (e.g., Pregill 1981), and, on the other hand, the view that these events took place in the late Mesozoic and early Tertiary, predominantly involved vicariance, and require a consideration of the distribution of land masses prior to the middle of the Cenozoic Era (e.g., Rosen 1976, MacFadden 1980). Recent studies of phylogenetically well-understood groups contain elements of both sides (MacFadden 1981, Cadle 1985).

Unlike the marine realm, with its spectacular if not always unequivocal fossil record, paleontologic evidence pertaining to the terrestrial debate is extremely sparse. Pregill (1981) was able to summarize only about ten instances of vertebrate fossils thought to bear on the question (although it is hard to see how some of the Cretaceous or Eocene occurrences he cites enable him to reach the conclusion that the groups in question arrived in the Antilles no earlier than the medial Tertiary). Land snails may prove to have the best fossil record of any terrestrial group.

A Mesozoic or early Tertiary occurrence of a taxon outside its modern Caribbean range disproves a Caribbean origin for that taxon in the later Tertiary. It provides a minimum age for the taxon and its sister-group, and likewise for any cladogenetic events lower down on the phylogenetic tree of its major group. The fossil occurrence of a taxon in North America does not mean that the same taxon was not also simultaneously present in the Caribbean region. For a tropical (i.e., thermally limited) taxon, the northern occurrence merely delineates the minimum northward extent of its range at the time. The contemporaneous southern, or equatorward, edge of the range may not be discoverable; the terrestrial fossil record in the Neotropics is not particularly promising in this regard. My working assumption in such cases is that the range extended as far toward the equator as the availability of land would permit.

Bishop (1979) produced a phylogenetic hypothesis for the American Camaenidae (Figure 18) based on the anatomical studies of Wurtz (1955) and summarized the fossil occurrences of American camaenids known to him, including a new species of *Caracolus* Montfort, 1810, from the Oligocene White River Group of Nebraska. The fossil evidence at that time suggested that *Caracolus* was differentiated in North America by the Oligocene at the latest; *Pleurodonte* Fischer von Waldheim, 1807 (in the broad sense, including *Pleurodontites* Pilsbry, 1939), was differentiated in Florida by the early Miocene (the age of the Tampa Limestone); and "differentiation of *Polydontes* and *Zachrysia* [could] best be understood in terms of modern geography and must post-date the period of dynamic geologic change" (Bishop 1979:282).

Solem (1978) stated that the presence of advanced features of apertural barriers, lip sinuation, and body whorl deflection in the Cretaceous and early Tertiary fossils *Kanabohelix* Pilsbry, 1927, and *Hodopoeus* Pilsbry and Cockerell, 1945, indicated that the initial radiation of the Camaenidae was completed by the end of the Mesozoic. He noted the resemblance to *Isomeria* of *Hodopoeus crassus* Pilsbry and Cockerell, 1945, and *H. hesperarche* (Cockerell, 1914), from unknown lower Tertiary localities in the American Southwest, but refrained from considering them congeneric because of their chronologic and geographic separation. With the recognition herein of *Labyrinthus* in the middle Eocene of California, such conservatism may no longer be necessary.

Roth (1984) recognized three camaenid genera and subgenera in the upper Eocene to lower Oligocene of Trans-Pecos Texas. *Pleurodonte* (*Pleurodonte*) and *P.* (*Dentellaria*) Schumacher, 1817, were sympatric in the Porvenir local fauna (late Eocene) of the Vieja Group. Their divergence and the subsequent dispersal that brought about their sympatry had already occurred by about 38 Ma before present. An indeterminate camaenid that is probably a member of the *Labyrinthus–Isomeria* lineage was present in the Whistler Squat local fauna in the same region of Texas approximately 10 Ma earlier.

The presence of *Zachrysia fraterna* in the late middle Eocene sets a minimum age for the differentiation of *Zachrysia*. It further sets a minimum age for the dichotomies farther down the cladogram: the divergence of the common ancestor of *Polydontes* and *Zachrysia* from *Pleurodonte,* and, still earlier, the divergences of the *Isomeria-Labyrinthus* and *Caracolus* lineages from the rest of the American Camaenidae. All of the earliest appearances of these genera are in North America.

Figure 19 shows the fossil occurrences of these camaenid genera relative to their modern distribution, plotted on the geography of middle Eocene time (48 Ma) (Sykes *et al.* 1982). The fossil and modern occurrences are connected by dotted lines—"tracks" in the parlance of vicariance biogeography (see Rosen 1976:432–433 for an explanation of method). In every case the tracks connect lower Tertiary localities in North America with Holocene ranges in the Caribbean region.

Except for Miocene *Pleurodonte* (*Pleurodonte*) in the Grenadines (Jung 1971) and Pliocene or younger *P.* (*Dentellaria*) in Jamaica (Bishop 1979), there is very little evidence for the timing of events at the southern ends of these tracks. Geological reconstructions of the Neotropics have paid little attention to the time when various Caribbean lands might have emerged above sea level (Hedges 1983). There is slightly better—although still indirect—control on the timing of extinctions in the north. Many lines of evidence show that the tropical biota was progressively restricted southward as the planetary temperature gradient steepened through the Tertiary (Savin 1977, Wolfe 1978). Miocene and later land mollusk faunas of western North America were dominantly composed of genera still extant in the region (Roth 1986).

Even though broadly drawn, these tracks are probably conservative estimates of the total ranges of their taxa. They may have overlapped much more extensively; that is, there may well have been much more sympatry between different camaenid genera. Sympatry of taxa now widely separated has been found repeatedly in Tertiary land mollusk faunas of western North America (Roth 1984, 1986). Through the Tertiary, the faunal elements came to inhabit different geographic areas. How much of this change represents sorting out along environmental gradients and how much represents historical accident is not clear. What determined, for instance, that *Zachrysia* should end up restricted to Cuba and *P.* (*Dentellaria*) to Jamaica? The allopatry on the Greater Antilles is all the more puzzling in light of the unusually high sympatric diversity shown by the land snail faunas of Jamaica and Hispaniola (Solem 1984).

The fossil evidence now available supports the model of a variety of camaenid genera, well differentiated by the middle Eocene, arrayed across the southern part of

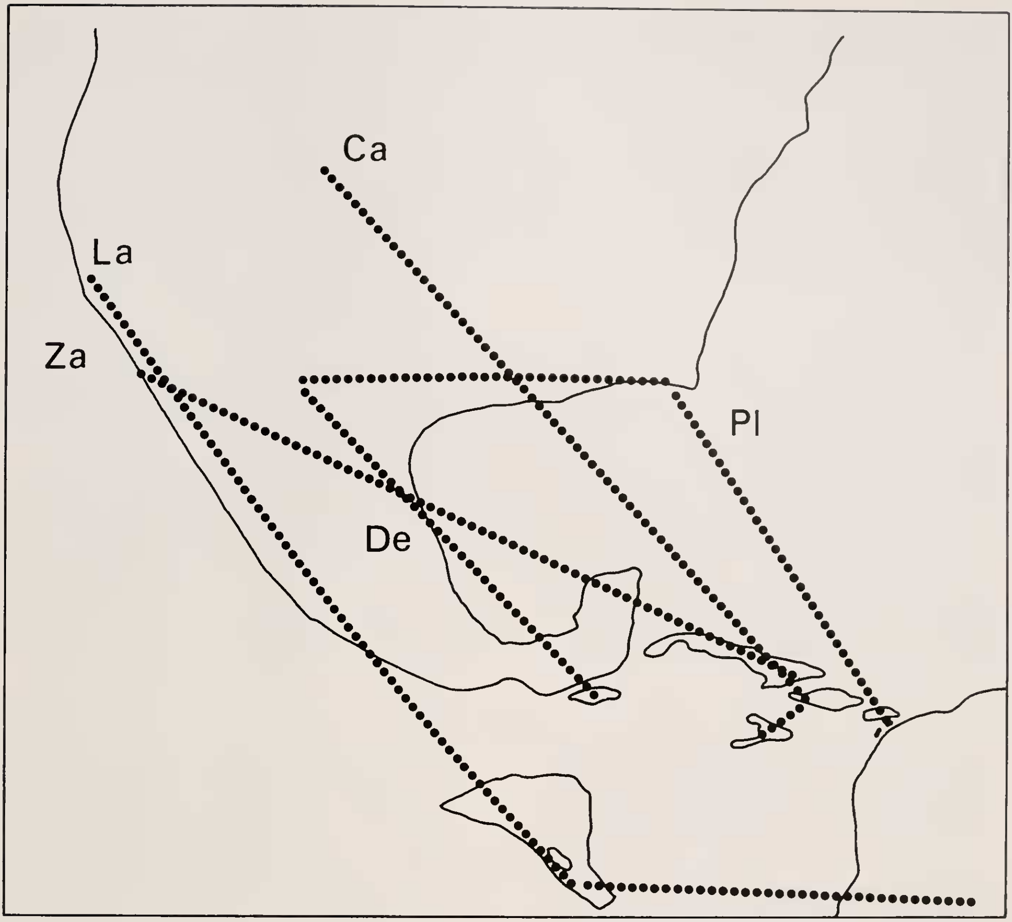


FIGURE 19. "Track record" of the American Camaenidae, plotted on map of land-mass distribution for the middle Eocene (48 Ma before present) (after Sykes *et al.* 1982). Dotted lines connect early to middle Tertiary occurrences of Camaenid genera with their Holocene ranges. Ca, *Caracolus*; De, *Pleurodonte* (*Dentellaria*); La, *Labyrinthus*; Pl, *Pleurodonte* (*Pleurodonte*); Za, *Zachrysia*.

North America, roughly parallel to the western limb of the Tethyan seaway. Through the Cenozoic, the northern, antitropical, margins of their ranges retreated southward; by the Holocene, if not earlier, they had become largely allopatric.

According to the phylogenetic hypothesis, *Zachrysia* is one of the most highly derived genera of the American Camaenidae; it is also the westernmost. The vicariant event that separated *Zachrysia* from *Polydontes* may have been related to the late Cretaceous or early Tertiary onset of arc volcanism in the American Southwest, east of the middle Eocene range of *Zachrysia* (Dickinson 1979: fig. 8; Minckley *et al.* 1986). The phylogenetic hypothesis and the known range of *Zachrysia* lead to the prediction that Eocene species assignable to *Polydontes* will be found in the southwestern United States or northern Mexico, east of the volcanic arc.

Zachrysia's position as a highly derived "end member" also suggests that any ancestral connection with the Australasian branch of the Camaenidae would have been eastward, along lands bordering the Tethyan seaway, rather than across the Pacific. Through the Eocene and the relevant parts of preceding geologic time, the Indopacific Ocean was much wider than today, spanning at least 210° at the equator, while only a narrow Atlantic Ocean separated America and Eurasia. The southern coasts of both continents lay in a warm and wet, monsoonal climatic belt (Frakes and Kemp 1972). The Australian Camaenidae are advanced relative to the southeast Asian members of the family; their ancestors entered Australia only after collision of the Australian and southeast Asian plates in the Miocene (Solem 1984). Many instances of biotic groups with this "interrupted Tethyan" type of distribution are known (Croizat 1964). If the American and Australasian camaenid groups are regarded as the two ends of this distribution, the prediction follows that fossil forms connecting the American with the Australasian Camaenidae will be found in Europe or western Asia.

Before anyone embarks on an all-out search, however, it would be well to reexamine the proposition that the American Camaenidae and the Australasian Camaenidae compose one monophyletic group and are not simply united by symplesiomorphies.

ACKNOWLEDGMENTS

I am grateful to T. A. Deméré, San Diego Natural History Museum, for bringing the fossil land mollusks from the Friars Formation to my attention and supplying needed information on their geologic setting. D. R. Lindberg helped with the interpretation of shell structure. R. L. Squires advised on Eocene biostratigraphy. E. C. Wilson loaned the type specimens of *H.? stocki.* J. E. Deisler contributed information on the status of introduced *Zachrysia* in Florida and the Bahamas. Photographs were taken in the University of California Museum of Paleontology and the Department of Invertebrate Zoology, California Academy of Sciences; the help of Jeanne M. Lynch is gratefully acknowledged. I also appreciate the comments of reviewers, named and anonymous, including L. R. Saul, G. L. Kennedy, and A. Solem.

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